

BEHAVIOR DURING SWARM MOVEMENT IN
STELOPOLYBIA AREATA
(HYMENOPTERA: VESPIDAE)

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INTRODUCTION

When a colony of bees or wasps leaves an old nesting site and moves to a new one it is faced with the problem of coordinating the movement of the individuals of the swarm so that all arrive at the new site. Scout honeybees (*Apis mellifera*) communicate the distance and direction of the new site by means of the same waggle dance used to communicate information about food sources (von Frisch, 1967). Martin G. Naumann has observed swarm movement in several species of Neotropical social wasps and has described behavior that suggests that scent marks are used to guide swarm members to a new site (Naumann, 1975).

The purpose of this paper is to present the author's own observations on behavior associated with swarm movement in *Stelopolybia areata*. The study was conducted during February 1973 at the Estación de Biología 'Los Tuxtlas' near San Andres Tuxtla, Veracruz, Mexico.

BEHAVIOR ASSOCIATED WITH SWARM MOVEMENT

The colony in which the behavior was observed had been constructing a new nest two meters up in a bush along a small arroyo in a cow pasture. On the morning of February 4 the adult population of several thousand was found to have abandoned the nest and to have settled on a twig of a large tree about 10 meters distant. The cause of the absconding was not certain, but several army ant (*Eciton* sp.) workers on the ground below the nest suggested that the nest may have been raided by a swarm of these ants earlier in the morning.

On the afternoon of the 4th and on each of the following three afternoons the swarm moved to a new site, providing an opportunity to observe its behavior. Data pertaining to each move are summarized in Table 1. The following description of the behavior of the wasps is extracted from the four days' observation.

Table I. Movement by a swarm of *Stelopolybia areata* on four successive days.

Date	Time	Direction	Distance	Terrain crossed	Height of bivouac	Characteristics of new site
4/II	1530	WSW	72m	along fence, then across tall grass and weeds	4m	tangle of lianas on trunk of large tree.
5/II	1730	NW	77m	tall 2nd growth, across arroyo into pasture	5m	split in trunk of dead tree.
6/II	1615	W	100m	pasture; across brushy arroyo	7m	tangle of lianas at top of small tree.
7/II	1650	NNW	70m	tall 2nd growth, along dirt road; across road into partially logged forest	8m	small twig near edge of crown of large tree.

In the mornings activity of the swarm was relatively low, though at least some wasps could always be seen flying within a meter or two of it. Observations of the swarm with a 60× telescope during these hours indicated that much of the activity was due to the arrival and departure of foragers. The approach of a forager would cause several wasps on the swarm to reach out toward the movement with their forelegs, while waving the antennae. When a forager landed she would immediately fold her wings, then often regurgitate liquid to these waiting workers. This behavior is identical to that observed on nests of the species. After such food exchanges the forager often disappeared into the midst of the swarm. The number of wasps engaged in foraging seemed to rise and fall with the appearance and disappearance of the sun in partly cloudy weather.

Though data collected from other colonies at the same time of year suggest that 5-12% of the swarm population should have been queens (Jeanne, 1973), no queens were ever visible on the surface of the swarm. Their morphological distinctiveness from workers (Jeanne and Fagen, 1974) should have made them discernible had they been there. It is likely that queens remained near the center of the swarm.

Toward midday workers could be seen flying about vegetation away from the swarm. As the afternoon wore on, these became more and more evident, and more so in a particular direction away from the swarm. These wasps seemed attracted to prominent objects in the environment — fenceposts, tall weeds or shrubs in the pasture, or leaves near the tips of twigs in tall second growth. In many instances they merely hovered a few centimeters from the object ("hovering"), but often they landed and walked about slowly with the head down and gaster up, antennating the surface over which they moved ("landing").

During the course of an afternoon activity at the swarm varied. Several times rapid increases in activity were observed during which great numbers of wasps took off and flew about in a large, diffuse cloud. During these times the numbers hovering at and landing on vegetation within 10-20 meters of the swarm often increased conspicuously. Within minutes, however, many of these wasps returned to the swarm and the activity dropped to its previous level.

As early as 1430 (February 7), two hours and twenty minutes before the swarm began to move on that day, a new kind of behavior was observed. Some of the workers landing on the upper parts of conspicuous objects walked rapidly over the surface, dragging the gaster continuously ("dragging"). The wings were usually buzzed, though sometimes this was interrupted with brief periods during which the wings were merely outstretched. The distance walked was usually in the range of 10-15 cm, taking 2-3 seconds, though there was much variation. At the end of a run the worker immediately took off.

Close observation of these individuals indicated that either the apical margin of the 5th (penultimate) sternite or the basal portion of the 6th was in contact with the substrate. Neither the tip of the gaster nor the sting made contact. The exposed surfaces of the fifth and sixth sternites are more or less uniformly covered with short hairs, and don't appear markedly different from other sternites in this regard. The basal portion of the 6th sternite, normally overlapped by the 5th, is hairless and quite smooth. In workers this region is noticeably more convex than in queens. Though it was not possible to confirm during observation, it may be this basal region that is in contact with the substrate.

Later in the afternoon the frequency of dragging increased, though not steadily. Often several workers could be seen performing it in a small area within a few minutes, then none would be seen for 15 or 20 minutes. By midafternoon the activities of hovering about, land-

ing on, and dragging the gaster over objects were very obviously concentrated in one direction away from the swarm. This was invariably the direction the swarm would take when it moved. On one occasion I was able to trace these activities to 60 meters in the direction the swarm would take nearly an hour later.

Meanwhile, changes could be observed in behavior at the swarm. The level of general activity was greater over that of the morning hours. Foragers could still be seen coming and going and exchanging with wasps in the swarm, but a new kind of activity was also occurring with increasing frequency. From time to time a worker landed on the swarm or on the substrate at the edge of the swarm and ran agitatedly among the wasps. During these runs the wings were buzzed and the gaster was held low, possibly touching the substrate, though this could not be confirmed, and frequently the gaster was wagged from side to side. Often the running wasp bumped into others, but without stopping. Sometimes, but not always, such behavior was followed by a noticeable increase in flight activity of the swarm as a whole.

Such periods of heightened activity, both at the swarm and away from it, occurred with increasing frequency until the swarm finally began to move. This usually began quite suddenly as more and more wasps began to take off and fly in large arcs at increasing distances from the swarm. Within five minutes all but a few hundred wasps had left the old site and were on their way toward the new one.

During movement of the swarm workers were frequently seen dragging on prominent objects; this was performed by wasps moving both to and from the new swarm site. Many wasps passing a given landmark; however, did not land, but merely hovered a few centimeters downwind of it before flying on in the direction of the new swarm site. Others landed and walked over the surface of the object with their gasters raised.

The moving swarm was so diffuse that it would not catch the attention of a person unaware of what was happening, even if he were standing in the path of movement. The passage of all the wasps past a point along the path took longer than 30 minutes.

The path followed by the swarm was usually a straight line, though on the first day it followed a row of fence posts south for the first 30 meters, then turned WSW toward the new site. Here there was only low grass along the direct route. Evidently the fence posts provided more suitable landmarks even though they did not lead directly to the new site. The path may be quite wide. On

one occasion I observed wasps landing on and dragging their gasters over objects as far apart as 10 meters along a line perpendicular to the direction of swarm movement.

On two occasions an attempt was made to determine when queens moved by netting samples of wasps as they passed a point along the route. Beginning at 1735 on 5 February the numbers of workers (queens in parentheses) netted in successive three-minute intervals were: 10 (0), 9 (0), 8 (0), 3 (2), 4 (2), 5 (0), 1 (1), 2 (1), 6 (1), 4 (0). On 6 February beginning at 1615 the results were 0 (0), 1 (0), 2 (0), 2 (0), 1 (1), 5 (1), 7 (0), 3 (0), 1 (0). The scanty results reflect the difficulty of netting wasps due to the diffuse nature of the moving swarm. Though sample sizes are small, the results suggest that queens do not begin moving to the new site until 10 or 15 minutes after the first workers begin to move.

The swarm could be followed only by moving from one dragging site to the next. It was possible to first roughly localize the new swarm site by noticing the point beyond which no wasps were observed dragging. Pinpointing the site was sometimes difficult, because of the rather wide path that was followed by the wasps. This was especially true in dense vegetation, where there were many possible sites available. It was usually possible to find the swarm by searching for unusually dense aggregations of flying wasps. Upon arrival of the bulk of the population at the new site the swarm usually settled down fairly quickly. This behavior made it much easier to locate the swarm in the new site while wasps were still arriving, rather than later. On some occasions arriving wasps seemed to overshoot their goal and could be seen searching beyond the new site. In one case several wasps were seen hovering about the tip of a dead tree some 11 meters beyond the newly settled swarm.

DISCUSSION

The behavior described herein is very similar to what Naumann has observed in *Polybia catillifex*, *P. oecodoma*, *Stelopolybia myrmecophila*, *Leipomeles dorsata*, and *Angiopolybia pallens* (Naumann, 1975). As Naumann concluded, it strongly suggests involvement of a trail pheromone. The dragging behavior could well function to deposit scent marks on prominent objects along the swarm route. Following swarm members may then pick up the scent by hovering downwind of such marks or by landing on marked objects and inspecting them with their antennae.

What is needed now is an experimental investigation of the whole matter, testing 1) whether such a scent trail is indeed produced and followed, 2) how the swarm is finally stimulated to begin moving, and 3) how individuals recognize the new site when they arrive.

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